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Résumé

With the internet, a massive amount of information on species abundance can be collected under citizen science programs. However, these data are often difficult to use directly in statistical inference, as their collection is generally opportunistic, and the distribution of the sampling effort is often not known. In this paper, we develop a general statistical framework to combine such "opportunistic data" with data collected using schemes characterized by a known sampling effort. Under some structural assumptions regarding the sampling effort and detectability, our approach allows to estimate the relative abundance of several species in different sites. It can be implemented through a simple generalized linear model. We illustrate the framework with typical bird datasets from the Aquitaine region, south-western France. We show that, under some assumptions, our approach provides estimates that are more precise than the ones obtained from the dataset with a known sampling effort alone. When the opportunistic data are abundant, the gain in precision may be considerable, especially for the rare species. We also show that estimates can be obtained even for species recorded only in the opportunistic scheme. Opportunistic data combined with a relatively small amount of data collected with a known effort may thus provide access to accurate and precise estimates of quantitative changes in relative abundance over space and/or time.

Keywords : opportunistic data, species distribution map, sampling effort, detection probability

1 Introduction

How species abundance varies in space and time is a major issue both for basic (biogeography, macroecology) and applied (production of biodiversity state indicators) ecology. Professionals working on biodiversity thus spend considerable resources collecting data that are suitable for estimating this variation (Yoccoz et al., 2001). Most of the scientific literature recommends the implementation of both a statistically valid sampling design and a standardized protocol for collecting such data (e.g. see Williams et al., 2002, for a review). Many methods have been developed to estimate species abundance in a defined location, e.g., using mark-recapture methods (Seber, 1982) or distance sampling approaches (Buckland et al., 1993). However, these approaches require an intense sampling effort and are not always practical. Many authors have noted that most frequently, interest will not be in abundance itself, but either in the rate of population change, i.e., the ratio of abundance in the same location at two different time points, or in the relative abundance, i.e., the ratio of abundance at two separate locations (MacKenzie and Kendall, 2002).

Relative abundance is frequently monitored with the help of simpler schemes. For instance, a set of sites is randomly sampled in the area of interest, and counts of organisms are organized on these sites using a given protocol. At a given location, the resulting count can be used as an index of the true abundance. Indeed, assuming constant detectability over space and time, the average number of animals counted per sampled site is proportional to the true abundance of the species in the area. Log-linear models can be used to represent this average number of animals detected per site as a function of space and/or time (and, possibly, other factors such as the habitat ; see for example van Strien and Pannekoek, 2001), and thereby, to infer population trends. Thus, such programs have been implemented in many countries to monitor the changes in the abundance of several groups of species, such as birds (e.g., for the French Breeding Bird Survey, see Julliard et al., 2004) or butterflies (e.g., for the European Butterfly Monitoring Scheme, see van Swaay et al., 2008). Estimates of relative abundance have also been commonly used for mapping the spatial distribution of several species (e.g., Gibbons et al., 2007).

In addition to such data characterized by a known sampling effort, a large amount of data can also be collected by non-standardized means, with no sampling design and no standardized protocol. In particular, the distribution of the observers and of their sampling effort is often unknown (Dickinson et al., 2010). These so-called "opportunistic data" have always existed, and with the recent development of citizen science programs, we observe a massive increase in the collection of these data on a growing number of species (e.g., Dickinson et al., 2010; Hochachka et al., 2012; Dickinson et al., 2012). Additionally, as the use of online databases facilitates the exchange and storage of data, such opportunistic data may now include millions of new observations per year that are collected in areas covering hundreds of thousands of square kilometres (e.g., the global biodiversity information facility, including more than 500 million records at the time of writing, see Yesson et al., 2007).

The temporal and spatial distributions of the observations in such data reflect unknown distributions of both observational efforts and biodiversity. Thus, a report of a high number of individuals of a given species at a given location compared to other locations could be because the focus species is abundant at this location or because numerous observers were present at this location. Using such opportunistic data to estimate changes in the space and time of species abundance is therefore complex, since any modeling approach should include a submodel of the observation process (Kéry et al., 2009; Hochachka et al., 2012) or an attempt to manipulate the data to remove the bias caused by unequal effort (see a discussion in Phillips et al., 2009).

As noted by MacKenzie et al. (2005), "In some situations, it may be appropriate to share or borrow information about population parameters for rare species from multiple data sources. The general concept is that by combining the data, where appropriate, more accurate estimates of the parameters may be obtained." In this paper, we propose a general framework which enables to combine data with known observational effort (which we call "standardized" data) with "opportunistic" data with an unknown sampling effort. We focus on multi-species and multi-site data that correspond to the data typically collected in this context.

The purpose of this study is to estimate the relative abundance of the species at different sites (different locations and/or times). We base this estimation on two datasets recording the number of animals detected by observers for each species of a pool of species of interest and each spatial unit of a study area of interest : (i) one "standardized" dataset is collected under a program characterized by a known

sampling effort, possibly varying among spatial units, (ii) one "opportunistic" dataset is characterized by a completely unknown sampling effort. We take into account the variation across species of their detectability, yet, as a first step, we assume that the observational bias towards some species are the same across the different sites. We show that, under this assumption, the information concerning both the distribution of the observational effort and the biodiversity can be efficiently retrieved from "opportunistic" data by combining them with standardized data. Moreover, we prove that such a combination returns more accurate estimates than when using the standardized data alone. Our statistical framework allowing this win-win combination can open numerous avenues for application. We used data on French birds, which are typical of existing data, to illustrate the numerous qualities of this framework. Note however that the work presented in this paper is a first step, and that further work will be required to fully account for varying observational bias towards some habitat types across the different sites.

During the reviewing process of this paper, we became aware of an independent and simultaneous work by Fithian et al. (2014) which develops similar ideas for combining multi-species and multi-sites data with thinned Poisson models.

2 Statistical modeling

We want to estimate the relative abundance (relative number of individuals) of I species in J sites. The "sites" j can either refer to different spatial sites, to different times, or to different combinations of sites and times. We suppose that we have access to K datasets indexed by k which gather counts for each species i at each site j. We have in mind a case where some datasets have been collected with some standardized protocol, while some others are of opportunistic nature.

Let X_{ijk} be the count of individuals of the species i by the observers in the site j in the dataset k. In this paper, we propose to model the counts X_{ijk} by

$$X_{ijk} \sim \text{Poisson}(N_{ij}P_{ik}E_{jk}), \quad \text{for } i = 1, \dots, I, \ j = 1, \dots, J \text{ and } k = 0, \dots, K-1, \tag{1}$$

where N_{ij} is the number of individuals (animals, plants, etc) of a species i at site j, and P_{ik}, E_{jk} are two parameters accounting for the bias induced by the observational processes. The parameter P_{ik} reflects both the detectability of the species i (some species are more conspicuous than others, some are more easily trapped, etc.) and the detection/reporting rate of this species in the dataset k (the attention of the observers may systematically vary among species). The parameter E_{jk} reflects the impact of the varying observational effort (including number and duration of visits, number of traps, etc.) and the varying observational conditions met during the counting sessions. In the next two sections, we explain the origin of our modeling, the hypotheses under which it is valid (see also the discussion Section 5), and we describe precisely the meaning of the two dimensionless parameters P_{ik} and E_{jk}. We refer to the Appendix A for a discussion on the link with models based on thinned Poisson processes. Before moving to these modeling issues, we point out that estimation can be easily carried out in the model (1), since it can be recast into a linear generalized model, see Section 2.4.

2.1 Count modeling

The count X_{ijk} of individuals of the species i in the site j for the dataset k is assumed to gather the counts from all visits in the site j. We assume that an individual is only counted *once during a single visit*, yet it can be counted *several times* in any dataset due to the possible *multiple visits* to a site j for a dataset k. In particular, we may have X_{ijk} larger than the number N_{ij} of individuals of the species i in the site j. In the following, we neglect identification errors and false positives.

For an individual a_{ij} of the species i in the site j and a visit v_{jk} in the site j for the dataset k, we define the random variable $Z_{a_{ij}v_{jk}}$ which equals 1 if the individual a_{ij} has been *seen and recorded* during the visit v_{jk}, and 0 otherwise. Assuming that there is no multiple count of an individual during a single visit, the count X_{ijk} is then given by

$$X_{ijk} = \sum_{v_{jk} \in \mathcal{V}_{jk}} \sum_{a_{ij}=1}^{N_{ij}} Z_{a_{ij}v_{jk}},$$

where $\mathcal{V}_{jk}$ is the set of all the visits v_{jk} in the site j for the dataset k. In the following, we denote by $p_{a_{ij}v_{jk}} = \mathbf{P}\left(Z_{a_{ij}v_{jk}} = 1\right)$ the probability for the individual a_{ij} to be seen and recorded during the visit v_{jk}.

If we assume that the random variables $\{Z_{a_{ij}v_{jk}} : a_{ij} = 1, \ldots, N_{ij} \text{ and } v_{jk} \in \mathcal{V}_{jk}\}$ are independent and that

$$\sum_{v_{jk}\in\mathcal{V}_{jk}} \sum_{a_{ij}=1}^{N_{ij}} p_{a_{ij}v_{jk}}^2 \quad \text{is small compared to} \quad \sum_{v_{jk}\in\mathcal{V}_{jk}} \sum_{a_{ij}=1}^{N_{ij}} p_{a_{ij}v_{jk}},$$

(which happens when $p_{a_{ij}v_{jk}}$ is small), then, according to Le Cam Inequality (Le Cam, 1960), the count X_{ijk} follows approximatively the Poisson distribution

$$X_{ijk} \sim \text{Poisson}\left(\sum_{v_{jk}\in\mathcal{V}_{jk}} \sum_{a_{ij}=1}^{N_{ij}} p_{a_{ij}v_{jk}}\right) = \text{Poisson}\left(N_{ij} \sum_{v_{jk}\in\mathcal{V}_{jk}} \bar{p}_{iv_{jk}}\right), \quad \text{with} \quad \bar{p}_{iv_{jk}} = \frac{1}{N_{ij}} \sum_{a_{ij}=1}^{N_{ij}} p_{a_{ij}v_{jk}}. \tag{2}$$

The parameter $\bar{p}_{iv_{jk}}$ corresponds to the average probability to detect and report during the visit v_{jk} an individual of the species i which has been sampled at random in the site j. We observe that the mean of the Poisson distribution

$$N_{ij} \sum_{v_{jk}\in\mathcal{V}_{jk}} \bar{p}_{iv_{jk}} = N_{ij} O_{ijk}$$

is the product of a first term N_{ij}, which is the number of individuals of the species i present in the site j, by a second term O_{ijk}, which is a nuisance term due to the observational process. We underline that the term O_{ijk} can be larger than 1 when the number V_{jk} of visits in the site j for the dataset k is large, since an individual can be counted several times during the V_{jk} visits.

2.2 Main modeling assumption

The main hypothesis of our modeling (1) is that the observational parameter O_{ijk} can be decomposed as

$$O_{ijk} = P_{ik} E_{jk}. \tag{3}$$

Let us give three examples where such a decomposition holds.

Example 1. (single habitat type) Assume that the ratios $\bar{p}_{iv_{jk}}/\bar{p}_{i'v_{jk}}$ depend only on the species i and i' and on the dataset k, so that $\bar{p}_{iv_{jk}}/\bar{p}_{i'v_{jk}} = \bar{p}_{iv'_{j'k}}/\bar{p}_{i'v'_{j'k}}$ for all i, i', j, j', v_{jk}, and $v'_{j'k}$. This means that the detection/reporting probability $\bar{p}_{iv_{jk}}$ of an individual of the species i during the visit v_{jk} can be decomposed as

$$\bar{p}_{iv_{jk}} = P_{ik} q_{v_{jk}}, \tag{4}$$

with P_{ik} the mean detection/reporting probability of the species i during a visit for the dataset k and $q_{v_{jk}}$ depending only on the visit v_{jk} (not on the species i). The parameter $q_{v_{jk}}$ represents the influence of the observational conditions during the visit v_{jk} on the detection/reporting probability. The parameter $q_{v_{jk}}$ is then a very complex function of the observational duration, the visibility conditions (weather conditions during the visit, vegetation met, etc.) and many other variables that affect the detection/reporting probability (number of traps, length of line transects, etc.). When the decomposition (4) holds, we have the decomposition (3) with $E_{jk} = \sum_{v_{jk}\in\mathcal{V}_{jk}} q_{v_{jk}}$.

The decomposition (4) enforces that the detection/reporting probability $\bar{p}_{iv_{jk}}$ does not depend on interactions between the species i and the visit v_{jk}. This property is quite restrictive and it is not likely to be met when several habitat types are present within a site j. Actually, if two visits v_{jk} and $v'_{j'k}$ take place in two different habitat types h_{jk} and $h'_{j'k}$ then the ratios $\bar{p}_{iv_{jk}}/\bar{p}_{i'v_{jk}}$ and $\bar{p}_{iv'_{j'k}}/\bar{p}_{i'v'_{j'k}}$ are not likely to be equal for all i and i' since some species may be specialized to the habitat type h_{jk} and some others to the habitat type $h'_{j'k}$. We can weaken the assumption (4) by allowing interactions $\epsilon_{iv_{jk}}$ between the species i and the visit v_{jk} as long as they cancel on average on each site j

$$\bar{p}_{iv_{jk}} = P_{ik} q_{v_{jk}} + \epsilon_{iv_{jk}}, \quad \text{with} \quad \sum_{v_{jk}\in\mathcal{V}_{jk}} \epsilon_{iv_{jk}} \simeq 0. \tag{5}$$

When (5) holds, we again have the decomposition (3) with $E_{jk} = \sum_{v_{jk} \in \mathcal{V}_{jk}} q_{v_{jk}}$. Such interactions $\epsilon_{iv_{jk}}$ can take into account heterogeneous observer attention bias toward the species i, but it does not allow for some systematic bias induced by heterogeneous habitat types. Actually, assume that the site j has two habitats h and h' and the site j' has only the habitat h'. Then if the species i (respectively i') is specialized to habitat type h (respectively h') we will have either $\sum_{v_{j'k}} \epsilon_{iv_{j'k}} < 0$ or $\sum_{v_{jk}} \epsilon_{i'v_{jk}} < 0$. So (5) cannot hold. The next two examples focus on the impact of heterogeneous habitat types.

Example 2. (known habitat types) Assume that for each count, we know in which habitat type it has occurred. Let us introduce the parameter $\widetilde{k} = (h, k)$ where h represents the habitat type h and k the dataset. For each dataset k, we can then pool together the counts occurring in the same site j and habitat type h. Let us denote by $X_{ij(h,k)}$ the counts of the species i in the site j, the habitat type h for the dataset k. We assume in the following that each visit occurs in a single habitat type : If not, we can artificially split a single visit in H different habitat types into H different visits, each occurring in a single habitat type.

Our main modeling assumption in this example is that the ratios $\bar{p}_{iv_{j(h,k)}}/\bar{p}_{i'v_{j(h,k)}}$ depend only on the species i and i', the dataset k and the habitat type h. This means that for each i, i', j, j' and $\widetilde{k} = (h, k)$ we have $\bar{p}_{iv_{j\widetilde{k}}}/\bar{p}_{i'v_{j\widetilde{k}}} = \bar{p}_{iv'_{j'\widetilde{k}}}/\bar{p}_{i'v'_{j'\widetilde{k}}}$ for all visits $v_{j\widetilde{k}}, v'_{j'\widetilde{k}}$ in the same dataset and the same habitat type. In this case, the probability $\bar{p}_{iv_{j(h,k)}}$ can be decomposed as

$$\bar{p}_{iv_{j(h,k)}} = P_{i(h,k)}\, q_{v_{j(h,k)}}, \tag{6}$$

with $P_{i(h,k)}$ the mean detection/reporting probability of a typical individual of the species i during a visit in the habitat type h for the dataset k and $q_{v_{j(h,k)}}$ not depending on i. We then have for $\widetilde{k} = (h, k)$

$$O_{ij\widetilde{k}} = P_{i\widetilde{k}} E_{j\widetilde{k}}, \quad \text{with} \quad E_{j\widetilde{k}} = \sum_{v_{j\widetilde{k}} \in \mathcal{V}_{j\widetilde{k}}} q_{v_{j\widetilde{k}}} \quad \text{and} \quad P_{i\widetilde{k}} = P_{i(h,k)} \quad \text{defined by (6).}$$

As above, we can allow some non-systematic heterogeneity by merely assuming that $\bar{p}_{iv_{j(h,k)}} = P_{i(h,k)}\, q_{v_{j(h,k)}} + \epsilon_{iv_{j(h,k)}}$ with $\sum_{v_{j(h,k)} \in \mathcal{V}_{j(h,k)}} \epsilon_{iv_{j(h,k)}} \simeq 0$.

Example 3. (homogeneous habitat type proportions) We assume again that each visit v_{jk} occurs in a single habitat type $h(v_{jk})$ (by artificially splitting non-homogeneous visits). Yet, we assume that this habitat type is not reported in the dataset. As in the second example, we also assume that the ratios $\bar{p}_{iv_{jk}}/\bar{p}_{i'v_{jk}}$ depend only on the species i and i', the dataset k and the habitat type $h(v_{jk})$. Hence, the probability $\bar{p}_{iv_{jk}}$ can be decomposed as

$$\bar{p}_{iv_{jk}} = P_{ih(v_{jk})k}\, q_{v_{jk}}, \tag{7}$$

with P_{ihk} the mean detection/reporting probability of a typical individual of the species i during a visit in the habitat type h for the dataset k and $q_{v_{jk}}$ not depending on i. Writing $\mathcal{V}_{jk}(h)$ for the set of the visits v_{jk} in the habitat type h we have

$$O_{ijk} = \sum_{h=1}^{H} \sum_{v_{jk} \in \mathcal{V}_{jk}(h)} \bar{p}_{iv_{jk}} = \sum_{h=1}^{H} P_{ihk} E_{jhk}, \quad \text{with} \quad E_{jhk} = \sum_{v_{jk} \in \mathcal{V}_{jk}(h)} q_{v_{jk}}.$$

The parameters E_{jhk} are likely to depend on h since there can be some observational bias towards some habitat types. If we assume that the observational bias is the same for each site j, which means that $E_{jhk}/E_{j'hk}$ does not depend on h, we have the decomposition

$$E_{jhk} = E_{jk} Q_{hk}, \tag{8}$$

where Q_{hk} reflects the observational bias towards the habitat type h in the dataset k. When the decompositions (7) and (8) hold, we have

$$O_{ijk} = \sum_{h=1}^{H} P_{ihk} Q_{hk} E_{jk} = P_{ik} E_{jk}, \quad \text{with} \quad P_{ik} = \sum_{h=1}^{H} P_{ihk} Q_{hk},$$

so O_{ijk} fulfills the decomposition (3). Again, as in the two first examples, we can weaken (7) by merely assuming that

$$\bar{p}_{iv_{jk}} = P_{ih(v_{jk})k}\, q_{v_{jk}} + \epsilon_{iv_{jk}}, \quad \text{with} \quad \sum_{v_{jk} \in \mathcal{V}_{jk}} \epsilon_{iv_{jk}} \simeq 0.$$

Let us explore when the decompositions (7) and (8) are likely to hold. We first observe that the decomposition (7) will be met as long as we include in the definition of the "habitat type" $h(v_{jk})$ all the exogenous variables which induces an interaction between the species i and the visit v_{jk}. The decomposition (8) is much more stringent. It requires that, for each dataset k, the observational bias towards some habitat types is the same across the different site j. It may not hold when the proportions on habitat types differ among the different sites. For example, if an habitat h is missing in a site j, then $E_{jhk} = 0$, so (8) cannot hold if $E_{j'hk} \neq 0$ for another site j'. An example where this property is more likely to be met is when the "sites" j correspond to the same spatial unit observed at different years j. In such a case, we can expect that the observational bias towards some habitat types remains stable years after years. When the observational bias towards some habitat types is not constant across the site, the decomposition (3) is not met in general. This case requires a substantial additional modeling that will be developed elsewhere.

Interpretation. Let us interpret more precisely the parameters P_{ik} and E_{jk} in the decomposition (3). Writing V_{jk} for the number of visits in the site j for the dataset k, we first observe that

$$\frac{1}{J}\sum_{j=1}^{J}\frac{1}{V_{jk}}\sum_{v_{jk}\in\mathcal{V}_{jk}}\bar{p}_{iv_{jk}} = \frac{1}{J}\sum_{j=1}^{J}\frac{O_{ijk}}{V_{jk}} = \frac{1}{J}\sum_{j=1}^{J}P_{ik}\frac{E_{jk}}{V_{jk}} = P_{ik}\bar{E}_k, \quad \text{with } \bar{E}_k = J^{-1}\sum_{j=1}^{J}E_{jk}/V_{jk}.$$

We can always replace (P_{ik}, E_{jk}) in the decomposition (3) by $(P'_{ik}, E'_{jk}) = (P_{ik}\bar{E}_k, E_{jk}/\bar{E}_k)$. Applying this renormalization step and dropping the prime (for notational simplicity), we obtain

$$P_{ik} = \frac{1}{J}\sum_{j=1}^{J}\frac{1}{V_{jk}}\sum_{v_{jk}\in\mathcal{V}_{jk}}\bar{p}_{iv_{jk}}, \tag{9}$$

which means that P_{ik} is the mean detection/reporting probability of a typical individual of the species i during a typical visit for the dataset k.

As explained in the three above examples, the parameter E_{jk} in (3) is a complex function of the conditions met during the visits in the site j for the dataset k, including the observational effort. This parameter E_{jk} can be (much) larger than 1 when the number V_{jk} of visits in the site j for the dataset k is very large. We point out that we can have E_{jk} very large even if O_{ijk} is smaller than 1, when the probability P_{ik} of detection/reporting of a typical individual of the species i is very small. In the remaining of the paper, we call *observational intensity* at the site j in the dataset k the parameter E_{jk}.

2.3 Identifiability issues

In the following, we deal with two datasets. A first dataset labeled by $k = 0$, in which we suppose that the observational intensities E_{j0} are known up to a constant. Henceforth, we will call this dataset the *standardized dataset*. We also consider a second dataset labeled by $k = 1$, characterized by unknown observational intensities E_{j1}. We will refer to this dataset as the *opportunistic dataset*.

2.3.1 A single opportunistic dataset is not enough

We consider first the case where we have a single dataset, i.e. $K = 1$. For notational simplicity, we drop the index k in this paragraph. Our observations X_{ij} then follows a Poisson distribution with intensity λ_{ij}, where $\lambda_{ij} = N_{ij}P_iE_j$. We cannot recover the $IJ + I + J$ parameters N_{ij}, P_i, and E_j from the IJ intensities λ_{ij}. Yet, if we are only interested by the relative abundances $N_{ij}/N_{ij'}$ with respect to a reference site, say $j' = 1$, can we recover the $I(J-1)$ ratios $\{N_{ij}/N_{i1} : j = 2, \dots, J,\ i = 1, \dots, I\}$ from the IJ parameters λ_{ij} ?

Let us write $\lambda_{ij} = \widetilde{N}_{ij}\widetilde{P}_i\widetilde{E}_j$ with $\widetilde{N}_{ij} = N_{ij}P_iE_1$, $\widetilde{P}_i = 1$ and $\widetilde{E}_j = E_j/E_1$. The parameters $\widetilde{N}_{ij}$ differ from the N_{ij} by a multiplicative constant P_iE_1 depending only on the species i. Therefore, we have $N_{ij}/N_{ij'} = \widetilde{N}_{ij}/\widetilde{N}_{ij'}$, which means that the parameters $\widetilde{N}_{ij}$ give access to the relative abundances N_{ij}/N_{i1} of the species i. When the dataset has been collected with a known sampling design, the observational intensity in a given site E_j is known up to an unknown constant, so that the ratios $E_j/E_{j'}$ are known and we can recover the $\widetilde{N}_{ij}$ (and hence the relative abundances) from λ_{ij} since the $\widetilde{P}_i$ and $\widetilde{E}_j$ are known. The situation is different with opportunistic datasets characterized by unknown ratios $E_j/E_{j'}$. In this

case, the $\widetilde{E}_j$ are also unknown, so we cannot recover the $\widetilde{N}_{ij}$ from the parameters λ_{ij}. Hence, we do not have access to the relative abundance N_{ij}/N_{i1}. As explained in the next paragraph, we need to combine different datasets.

2.3.2 Combining an opportunistic dataset with a standardized one

Let us now investigate the identifiability issues when we combine a standardized dataset (labeled by $k = 0$) with an opportunistic one (labeled by $k = 1$). In this case, we have $2IJ$ parameters $\lambda_{ijk} = N_{ij}P_{ik}E_{jk}$ for $IJ+2(I+J)$ parameters N_{ij}, P_{ik} and E_{jk}. For $IJ > 2(I+J)$, which typically holds for large J and $I \geq 3$, we have more parameters λ_{ijk} than parameters N_{ij}, P_{ik} and E_{jk}. Nevertheless, as explained in the Appendix B, the model is not identifiable without $J+I+1$ additional identifiability conditions. As in Section 2.3.1, we introduce some renormalisation $\widetilde{N}_{ij}$, $\widetilde{E}_{jk}$ of $\widetilde{P}_{ik}$ of N_{ij}, E_{jk} and P_{ik}, which enables us to easily express these identifiability conditions while preserving the identity $\widetilde{N}_{ij}\widetilde{E}_{jk}\widetilde{P}_{ik} = \lambda_{ijk} = N_{ij}E_{jk}P_{ik}$.

In the following, we assume that the ratios $\{E_{jk}/E_{j'k} : j \neq j'\}$ are known for the dataset $k = 0$ (standardized dataset), but not for the dataset $k = 1$ (opportunistic one). As above, we define $\widetilde{E}_{j0} = E_{j0}/E_{10}$ (which is known) and $\widetilde{P}_{i1} = 1$ for all i. We could have set $\widetilde{P}_{i0} = 1$ instead of $\widetilde{P}_{i1} = 1$, but the latter choice is more suited for handling species i monitored in the dataset $k = 1$ but not in the dataset $k = 0$, as we will show later. We must still set one more constraint. We choose $\widetilde{P}_{10} = 1$ for convenience. These $I + J + 1$ constraints combined with the identity $\widetilde{N}_{ij}\widetilde{E}_{jk}\widetilde{P}_{ik} = \lambda_{ijk} = N_{ij}E_{jk}P_{ik}$ lead to the change of variables :

$$\begin{aligned} \widetilde{N}_{ij} &= N_{ij}P_{i1}E_{10}\frac{P_{10}}{P_{11}}, \\ \widetilde{E}_{jk} &= \frac{E_{jk}}{E_{10}} \times \frac{P_{1k}}{P_{10}} \\ \widetilde{P}_{ik} &= \frac{P_{ik}}{P_{i1}} \times \frac{P_{11}}{P_{1k}}. \end{aligned} \tag{10}$$

In terms of these new variables, we have the simple statistical model $X_{ijk} \sim \text{Poisson}(\widetilde{N}_{ij}\widetilde{E}_{jk}\widetilde{P}_{ik})$ with $\widetilde{E}_{j0} = E_{j0}/E_{10}$ for all j, $\widetilde{P}_{i1} = 1$ for all i and $\widetilde{P}_{10} = 1$. These $J + I + 1$ quantities are known, and the resulting statistical model is identifiable.

Let us interpret these new quantities. The parameter $\widetilde{N}_{ij}$ is proportional to the abundance N_{ij} by an unknown factor $P_{i1}E_{10}P_{10}/P_{11}$ depending only on the species i. As in Section 2.3.1, these parameters give access to the relative abundance $N_{ij}/N_{i1} = \widetilde{N}_{ij}/\widetilde{N}_{i1}$ of each species i in each site j. The parameters $\widetilde{E}_{j1}$ are equal, up to a constant, to the observational intensity E_{j1} ; therefore, they provide the relative observational intensities E_{j1}/E_{11} for each site j in the dataset 1. Finally, $\widetilde{P}_{i0}$ is proportional to the ratio P_{i0}/P_{i1} by an unknown factor P_{11}/P_{10}, so we can compare the ratios P_{i0}/P_{i1} across the different species. The ratio P_{i0}/P_{i1} reflects the systematic difference of attention toward some species among the observers of the two schemes.

In addition, we emphasize that we can consider the case where some species i are not monitored in the dataset 0 but are recorded in the dataset 1. This case can be handled by merely adding the constraints $\widetilde{P}_{i0} = P_{i0} = 0$ for the concerned species i.

2.4 Estimation via a Generalized Linear Model

We can estimate the parameters $\widetilde{N}_{ij}$, $\widetilde{E}_{jk}$ and $\widetilde{P}_{ik}$ by the maximum likelihood estimators $(\widehat{N}_{ij}, \widehat{E}_{jk}, \widehat{P}_{ik})$ with the constraints $\widehat{E}_{j0} = \widetilde{E}_{j0}$ for all j, $\widehat{P}_{i1} = 1$ for all i and $\widehat{P}_{10} = 1$. This estimation can be carried out with the help of a generalized linear model. Indeed, with the notations $n_{ij} = \log(\widetilde{N}_{ij})$, $e_{jk} = \log(\widetilde{E}_{jk})$ and $p_{ik} = \log(\widetilde{P}_{ik})$, Model (1) can be recast as a classical generalized linear model from the Poisson family with a log link :

$$X_{ijk} \sim \text{Poisson}(\lambda_{ijk}), \quad \text{with } \log(\lambda_{ijk}) = n_{ij} + e_{jk} + p_{ik}. \tag{11}$$

Indeed, we only have to define $e_{j0} = \log \widetilde{E}_{j0}$ as a known offset in the model, $p_{i1} = 0$ for all i, and fit the resulting model with any statistical package (see Supplementary materials).

3 Theoretical gain of combining two datasets

It is important to investigate whether the estimates of the relative abundance obtained by combining the dataset 1 with unknown observational intensity ratios $E_{j1}/E_{j'1}$ to the dataset 0 with known observational intensity ratio $E_{j0}/E_{j'0}$ improves upon the estimates obtained with the single dataset 0. In this section, we investigate this issue analytically. An improvement is expected simply by looking at the balance between the number of observations and the number of free parameters. With the dataset 0, we have IJ observations, and we want to estimate IJ free parameters ; whereas with the two datasets 0 and 1, we have $2IJ$ observations for $IJ + J + I - 1$ free parameters. The balance between the number of observations and the number of free parameters is better in the second case. Below, we quantify the theoretical improvement more precisely by comparing the variance of the maximum-likelihood estimators in the two cases. Then, we show that dataset combination also allows to estimate relative abundance for species i not monitored in the dataset 0.

3.1 Variance reduction

For mathematical simplicity, we assume in the following that the ratios P_{i0}/P_{i1} are known for all i. In terms of the normalized variables, this means that the $\widetilde{P}_{i0}$ are known.

When we work with the single dataset 0, we can estimate $\widetilde{N}_{ij}$ with the maximum likelihood estimator $\widehat{N}^0_{ij} = X_{ij0}/(\widetilde{E}_{j0}\widetilde{P}_{i0})$. Let us investigate how the maximum likelihood estimator $\widehat{N}_{ij}$ associated with the model $X_{ijk} \sim \text{Poisson}(\widetilde{N}_{ij}\widetilde{E}_{jk}\widetilde{P}_{ik})$ improves upon $\widehat{N}^0_{ij}$. We consider the case where the (unknown) observational intensities E_{j1} in the dataset 1 is much larger than the observational intensities E_{j0} in the dataset 0. Hence, we consider the asymptotic setting where E_{j1} goes to infinity. In the Appendix B, we show that the limit variance of $\widehat{N}_{ij}$ when $E_{j1} \to \infty$ is given by

$$\text{var}(\widehat{N}_{ij}) \overset{E_{j1}\to\infty}{\to} \text{var}(\widehat{N}^0_{ij}) \times \frac{P_{i0}N_{ij}}{\sum_l P_{l0}N_{lj}} \,. \tag{12}$$

In particular, the variance of the estimate is reduced by a factor

$$\frac{\text{var}(\widehat{N}_{ij})}{\text{var}(\widehat{N}^0_{ij})} \overset{E_{j1}\to\infty}{\approx} \frac{P_{i0}N_{ij}}{\sum_l P_{l0}N_{lj}} \,,$$

when working with the two datasets instead of the sole dataset 0. This factor can be very small for rare species (N_{ij} small), hardly detectable species (P_{i0} small), or when the number I of monitored species is large.

Let us explain the origin of this variance reduction in the simple case where the ratios P_{i0}/P_{i1} are the same for all the species i (which formally corresponds to $\widetilde{P}_{i0} = 1$ for all i). In this case, we have a closed-form formula for $\widehat{N}_{ij}$ (see Formula (21) in the Appendix B)

$$\widehat{N}_{ij} = \frac{X_{ij0} + X_{ij1}}{\sum_l (X_{ij0} + X_{lj1})} \times \frac{\sum_l X_{lj0}}{\widetilde{E}_{j0}} \,,$$

which reveals the contribution of each dataset to the estimation of the (normalized) relative abundance. Actually, the estimator $\widehat{N}_{ij}$ is the product of two terms, where the first term mainly depends on the opportunistic dataset 1 when the observational intensities E_{j1} are large, whereas the second term only depends on the dataset 0

$$\widehat{N}_{ij} \overset{E_{j1}\to\infty}{\approx} \frac{X_{ij1}}{\sum_l X_{lj1}} \times \frac{\sum_l X_{lj0}}{\widetilde{E}_{j0}} \,.$$

Let us interpret these two terms. The first ratio on the right-hand side provides an estimation of the proportion $\widetilde{N}_{ij}/\sum_l \widetilde{N}_{lj}$ of individuals in a site j that belong to a species i. This proportion is estimated by the ratio of the number X_{ij1} of individuals of the species i observed at site j in the opportunistic dataset to the total number $\sum_l X_{lj1}$ of individuals observed at site j in the same data. When the observational intensities E_{j1} in the opportunistic dataset 1 is large, the ratio $X_{ij1}/\sum_l X_{lj1}$ provides a very accurate

estimation of the abundance proportion $\widetilde{N}_{ij}/\sum_l \widetilde{N}_{lj}$, and we have (see Formula (22) in the Appendix B)

$$\widehat{N}_{ij} \overset{E_{j1}\to\infty}{\approx} \frac{\widetilde{N}_{ij}}{\sum_l \widetilde{N}_{lj}} \times \frac{\sum_l X_{lj0}}{\widetilde{E}_{j0}}\,. \tag{13}$$

The second term in the right-hand side of (13) provides an estimation of the total (normalized) relative abundance $\sum_l \widetilde{N}_{lj}$ at the site j. This total (normalized) abundance is estimated from the dataset 0 by dividing the total number $\sum_l X_{lj0}$ of individuals counted at the site j in the dataset 0 by the (normalized) observational intensity $\widetilde{E}_{j0}$. Let us now explain the reduction of variance observed in (12). The formula (13) shows that we estimate $\widetilde{N}_{ij}$ by first estimating the total (normalized) relative abundance $\sum_l \widetilde{N}_{lj}$ with the dataset 0 and then renormalize this estimation with the ratio $\widetilde{N}_{ij}/\sum_l \widetilde{N}_{lj}$ which has been accurately estimated with the dataset 1. The reduction of variance observed in (12) then results from the use of the whole counts $\sum_l X_{lj0}$ at site j in the dataset 0 for estimating $\widetilde{N}_{ij}$ instead of the sole counts X_{ij0} of the species i at site j.

3.2 Species not monitored in the scheme characterized by a known sampling observational intensity

As already mentioned, combining the two datasets also allows to estimate $\widetilde{N}_{ij}$ for some species i that are not monitored in the dataset 0, but are monitored in the opportunistic dataset 1. This situation formally corresponds to the case where $P_{i0} = 0$. For $E_{j1} \to \infty$, the limit variance of the estimator $\widehat{N}_{ij}$ is (see Formula (25) in the Appendix B)

$$\mathrm{var}(\widehat{N}_{ij}) \overset{E_{j1}\to\infty}{\sim} \frac{\widetilde{N}_{ij}^2}{\sum_l \widetilde{P}_{l0}\widetilde{N}_{lj}\widetilde{E}_{j0}}.$$

Because the species i is not monitored in dataset 0, the (normalized) relative abundance $\widetilde{N}_{ij}$ cannot be estimated with the sole dataset 0. Thus, there is an obvious improvement to be made by using our estimation scheme that combines the two datasets. To reveal the power of our approach, let us compare the variance $\mathrm{var}(\widehat{N}_{ij})$ of our relative abundance estimator with the variance of the imaginary estimator $\widehat{N}_{ij}^{0,\mathrm{imaginary}}$ based on an imaginary dataset 0 where the species i would have been monitored with some (imaginary) detection/reporting probability $P_{i0}^{\mathrm{imaginary}}$. The variance of the maximum likelihood estimator $\widehat{N}_{ij}^{0,\mathrm{imaginary}}$ of $\widetilde{N}_{ij}$ with this imaginary dataset 0 would be $\widetilde{N}_{ij}/(\widetilde{E}_{j0}\widetilde{P}_{i0}^{\mathrm{imaginary}})$ so that

$$\mathrm{var}(\widehat{N}_{ij}) \overset{E_{j1}\to\infty}{\sim} \mathrm{var}(\widehat{N}_{ij}^{0,\mathrm{imaginary}}) \times \frac{P_{i0}^{\mathrm{imaginary}} N_{ij}}{\sum_l P_{l0} N_{lj}}\,.$$

In particular, the estimation provided by $\widehat{N}_{ij}$ can significantly outperform the imaginary estimation we would have obtained with the sole imaginary dataset 0 (where the species i would have been monitored). Moreover, if we compare the estimator $\widehat{N}_{ij}$ with the imaginary estimator $\widehat{N}_{ij}^{\mathrm{imaginary}}$ based on both the imaginary dataset $k = 0$ and the dataset $k = 1$, we observe that the ratio of their variance

$$\frac{\mathrm{var}(\widehat{N}_{ij})}{\mathrm{var}(\widehat{N}_{ij}^{\mathrm{imaginary}})} = \frac{P_{i0}^{\mathrm{imaginary}} N_{ij} + \sum_l P_{l0} N_{lj}}{\sum_l P_{l0} N_{lj}}$$

remains close to one when $P_{i0}^{\mathrm{imaginary}} N_{ij} \ll \sum_l P_{l0} N_{lj}$. This means that with our estimation scheme, there is not much difference between the estimation based on a dataset collected with known observational intensities where a species i is rare and the estimation based on a dataset collected with known observational intensities where a species i is not monitored. In other words, there is no instability on the estimation of the relative abundance of a species when it is not present in the dataset collected with known observational intensities.

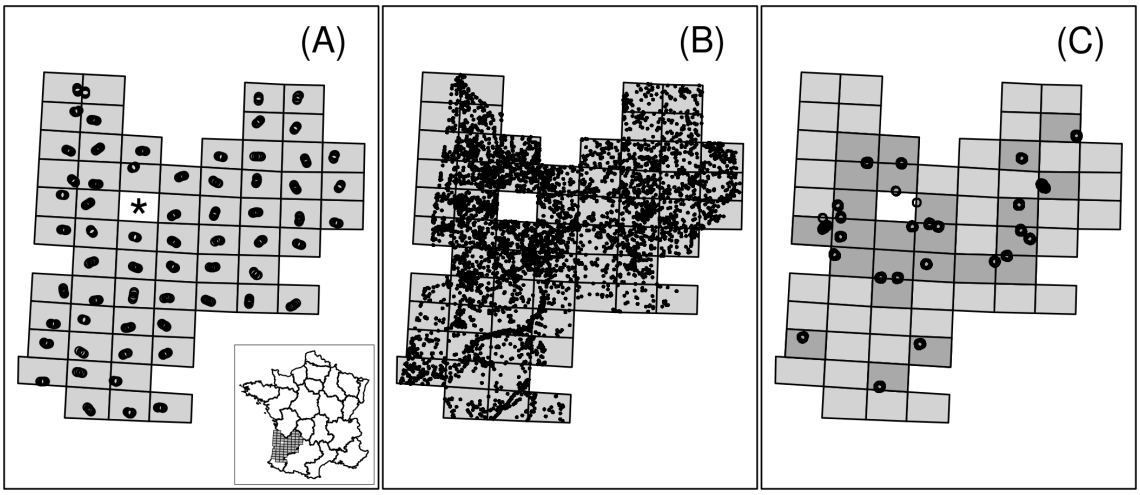

FIGURE 1 – The datasets used to illustrate our statistical framework. The location of the Aquitaine region in France is displayed in the insert. (A) distribution of the ACT listening points in the region ; (B) distribution of the LPO records (opportunistic dataset) in the region ; (C) distribution of the STOC listening points in the region. The grey quadrat cells are used as the "sites" in our analysis (they measure $\approx 30 \times 20$ km). Note that the quadrat cell containing the Bordeaux metropolitan area (indicated by an asterisk in (A)) has been removed from the dataset.

4 Illustration

4.1 Datasets

In this section, we investigate on some datasets the predictive power of our modeling approach. We estimated the relative abundance of 34 bird species in the non-urban habitat of 63 sites in the Aquitaine region (South West of France). We fitted our model with an opportunistic dataset and a dataset collected with known observational intensity. We then assessed the predictive power of our approach with the help of an independent dataset collected with known observational intensity in the same area, hereafter referred as "validation dataset". We therefore illustrate the ability of our approach to provide better predictions of species relative abundance than other approaches based on either of the two datasets alone.

We first describe the opportunistic dataset. We used the recent online database developed by the Ligue de Protection des Oiseaux (LPO, Bird Life representative in France, largest French bird watcher NGO, with regional delegations). This online system was launched successively by the different regional LPO groups, and we acquired data from one of the first groups to start, Aquitaine, South-Western France, with data collection starting in 2007 (www.fauneaquitaine.org). Any citizen who can identify bird species can register on this website and record any bird observation s/he wishes, noting the species, date, and location (to the nearest 500 m). Hundreds of observers thus record hundreds of thousands observations. We typically ignore why these observations were made, e.g., the motivation of the observer, the reason for choosing to report these observations over others, whether they report all the species they have seen at a given place and time, the underlying observational intensity, etc. We selected all such opportunistic records between April and mid-June 2008–2011. For each record, we considered the number of animals detected by the observer. Data were pooled over years, because we will focus here only on spatial variation in relative abundance. Over 115 000 species records detected in a non-urban habitat were considered in this study (see Fig. 1B).

We then describe the dataset collected with known observational intensity, used for the fit of the model. We used the data from the ACT monitoring plan jointly carried out by the French National Game and Wildlife Agency (ONCFS, Office National de la Chasse et de la Faune Sauvage), the national hunter association (FNC, Fédération Nationale des Chasseurs) and the French departemental hunters associations (FDC, Fédérations Départementales des Chasseurs). The main objective of the ACT survey was to monitor the breeding populations of several migratory bird species in France (Boutin et al., 2003) ; ACT stands for *Alaudidae*, *Columbidae*, *Turdidae*, which were the main bird clades of interest for this

monitoring, though this program also monitors several *Corvidae* species (see table 1 for the list of species of interest for our study). Thus, only a fraction of the species recorded by the LPO program was also studied by the ACT survey. The Aquitaine region was discretized into 64 quadrat cells, and in each cell, a 4km long route was randomly sampled in the non-urban habitat of the cell (see Fig. 1(A)). Each route included 5 points separated by exactly 1 km. Each route was traveled twice between April and mid-June, and every point was visited for exactly 10 minutes within 4 hours after sunrise in appropriate weather conditions. Every bird heard or seen was recorded, and for each point and each species, the maximum count among the two visits was retained. The observers were professionals from the technical staff of either the ONCFS or the hunters associations. Note that due to organization constraints, some listening points in a site were not necessarily counted every year. Between 2008 and 2011, over 9 500 birds were counted.

Finally, we describe the validation dataset, used to assess the predictive power of our model. We used the data from the STOC program (*Suivi temporel des oiseaux communs*), a French breeding bird survey carried out by the French museum of natural history (MNHN, Museum National d'Histoire Naturelle) for the same region and the same years. The STOC survey (Jiguet et al., 2012) is based on a stratified random sampling, with each volunteer observer being assigned a 2×2 km square randomly chosen within 10 km of his house. The observer then homogeneously distributed 10 points within the square. Each point was visited twice between April and mid-June (before and after May 8th, with at least 4 weeks between visits) for exactly 5 minutes within 4 hours after sunrise in appropriate weather conditions (no rain or strong winds). Every bird heard or seen was recorded, and for each point and each species, the maximum count among the two visits was retained. These counts were then summed for a given square, year and species. Between 2008 and 2011, 251 listening points belonging to 29 such squares have been surveyed in non-urban habitat (to allow the comparison with the other datasets, we removed the listening points located in urban habitat), most of them for several years, and over 15241 birds were detected by the observers.

Our aim was to test our model ability to provide a better prediction of the spatial variation in species relative abundance than any model based on either of the two datasets alone. The "sites" of our model were the 63 quadrat cells defined for the ACT survey ; we removed the quadrat cell containing the metropolitan area of Bordeaux (a large town with a population of > 1 million inhabitants), where the sampling process in the opportunistic dataset could not be supposed to be the same as in the other areas (see Fig. 1(A)). We focused on $I = 34$ bird species (see Table 1). Note that the smaller number of species monitored in the ACT survey allowed to demonstrate the ability of our approach to estimate the relative abundance of species monitored only in opportunistic dataset. For both the ACT survey and the STOC survey, the observational intensity in the site j was measured as the number of points-years sampled in the quadrat cell j during the period 2008–2011. We used the validation STOC dataset to assess the predictive power of our modeling approach. Only 24 sites contained at least one STOC listening point (Fig. 1(C)), so that this assessment was restricted to these sites.

4.2 Comparison of the predictive power

Let X_{ijk} be the number of animals of the species i detected in the site j in the dataset k. Let $k = a$ denote the dataset with known observational intensity collected by the ACT survey ; let $k = \ell$ denote the opportunistic dataset collected by the LPO ; finally, let $k = s$ denote the validation dataset collected by the STOC survey. We compared different statistical approaches to estimate the relative abundances of the species in the sites.

Let $\widehat{N}_{ij}^{m}$ be the relative abundance estimated for the species i in the site j with the statistical approach m. We estimated the relative abundance of each species i in each site j with the following approaches :

$$\widehat{N}_{ij}^{a} = X_{ija}/\pi_j^a \tag{14}$$

$$\widehat{N}_{ij}^{s} = X_{ijs}/\pi_j^s \tag{15}$$

$$\widehat{N}_{ij}^{\ell 1} = X_{ij\ell}/S_j \tag{16}$$

$$\widehat{N}_{ij}^{\ell 2} = X_{ij\ell}/\sum_i X_{ij}^{\ell} \tag{17}$$

TABLE 1 – List of the 34 bird species under study. The 13 species monitored only by the ACT survey are indicated by an asterisk. All species were surveyed by the STOC and the LPO program.

Latin name	species
Aegithalos caudatus	Long-Tailed Tit
*Alauda arvensis**	Eurasian Skylark
*Alectoris rufa**	Red-Legged Partridge
Carduelis carduelis	European Goldfinch
Carduelis chloris	European Greenfinch
Certhia brachydactyla	Short-Toed Treecreeper
*Columba palumbus**	Common Wood Pigeon
*Coturnix coturnix**	Common Quail
Cuculus canorus	Common Cuckoo
Dendrocopos major	Great Spotted Woodpecker
Erithacus rubecula	European Robin
Fringilla coelebs	Common Chaffinch
*Garrulus glandarius**	Eurasian Jay
Hippolais polyglotta	Melodious Warbler
*Lullula arborea**	Woodlark
Luscinia megarhynchos	Common Nightingale
Milvus migrans	Black Kite
Cyanistes caeruleus	Eurasian Blue Tit
Parus major	Great Tit
Passer domesticus	House Sparrow
*Phasianus colchicus**	Common Pheasant
Phoenicurus ochruros	Black Redstar
Phylloscopus collybita	Common Chiffchaff
*Pica pica**	Eurasian Magpie
Pica viridis	Eurasian Green Woodpecker
Sitta europaea	Eurasian Nuthatch
*Streptopelia decaocto**	Eurasian Collared Dove
*Streptopelia turtur**	European Turtle Dove
Sylvia atricapilla	Eurasian Blackcap
Troglodytes troglodytes	Eurasian Wren
*Turdus merula**	common Blackbird
*Turdus philomelos**	Song Thrush
*Turdus viscivorus**	Mistle Thrush
Upupa epops	Eurasian Hoopoe

where π_j^k denotes the number of listening points of the site j sampled in the dataset k, and S_j denotes the area of the site j (determined by intersecting each ACT quadrat with the Aquitaine region). For the LPO dataset $k = \ell$, we had to account for the site-specific unknown intensity. We estimated this intensity with two proxies that are commonly used in such cases. First, we assumed that observational intensity was spatially uniform so that it varied only with quadrat cell area S_j (the resulting approach is labeled $\ell 1$). Another proxy considered that the observational intensity within a site was proportional to the total number of records across the sites (pooled over all species ; the resulting approach is labeled $\ell 2$).

Finally, we fitted the model described in the previous sections, using the ACT dataset a as the dataset collected with known observational intensity ($k = 0$), and the LPO dataset ℓ as the opportunistic dataset ($k = 1$). Note that we supposed a quasi-Poisson distribution, to account for moderate overdispersion in our dataset. Thus, we could estimate the value of $\widehat{N}_{ij}^{\ell+a}$ with our approach.

The relative abundance is the absolute abundance multiplied by an unknown constant, and this constant may vary among approaches. Therefore, to allow the comparison between the various approaches, we standardized the relative abundance estimates in the following way :

$$\widetilde{N}_{ij}^{m} = \frac{\widehat{N}_{ij}^{m}}{\sum_j \widehat{N}_{ij}^{m}}$$

We want to investigate whether the estimates obtained by our model are closer or not to the true densities than any of the estimates that could be obtained from the individual datasets. We used the value $\widetilde{N}_{ij}^{s}$ estimated with the validation STOC dataset as the value of reference. We assessed the predictive power of each approach m by calculating, for each species, the Pearson correlation coefficient between the standardized relative abundance $\widetilde{N}_{ij}^{m}$ estimated with the method m and the standardized relative abundance $\widetilde{N}_{ij}^{s}$ estimated with the validation dataset. We summarized this power by calculating the median and interquartile range (IQR) of these coefficients over the different species of interest. Although the relative abundance estimates were calculated on the complete dataset, these results were presented by separating the species monitored in the ACT survey, and the species not monitored in this survey. This allowed to evaluate the ability of our approach to estimate the relative abundance of species not monitored in the standardized dataset.

We also investigated the stability of our statistical approach when the standardized dataset is small. We therefore assessed this stability by replacing our big standardized ACT dataset a by a much smaller dataset a'. We subsampled the dataset a : for each site, we randomly sampled only one listening point in every site, and we considered the bird counts of only one randomly sampled year for every point. Thus, we artificially divided the observational intensity by 18 in average in this dataset : the complete ACT dataset a stored the bird counts carried out in 1107 listening points-years, whereas the reduced dataset a' stored the bird counts carried out in only 63 listening-points-years (one in every site). We also estimated the standardized relative abundance $\widetilde{N}_{ij}^{a'} = X_{ij}^{a'} / \sum_j X_{ij}^{a'}$ with this reduced dataset. Finally, we estimated the relative abundance $\widetilde{N}_{ij}^{\ell+a'}$ by combining this reduced standardized dataset with the opportunistic dataset according to our model. We also assessed the predictive power of these two approaches by comparing the estimates with the reference values obtained with the STOC dataset.

The online supplementary material contains the data and the code for the R software (R Core Team, 2013) that will allow the reader to reproduce our calculations.

4.3 Results

We fitted our model on the LPO and ACT datasets. There was only a small amount of overdispersion in our data (the coefficient of overdispersion was equal to 1.22) ; the examination of the residuals did not reveal any problematic pattern and the quality of the fit was satisfying. We observe in table 2 that the predictive power was larger for our statistical approach than for all other approaches, whether based on the dataset a or ℓ alone.

The predictive power of our statistical approach did not decrease much when model was fit on the smaller standardized dataset a', despite the fact that the observational intensity in this dataset was divided by about 20. In particular, the predictive power of our approach with a reduced dataset remained larger than the predictive power of the other approaches. We observe a strong positive correlation bet-

TABLE 2 – Predictive capabilities of the various possible approaches to estimate the relative abundance of 34 bird species in 63 sites in the Aquitaine region. For each possible estimation approach m, we present the median (calculated over the species) of the Pearson's correlation coefficient between the relative abundance $\widetilde{N}_{ij}^{m}$ estimated by the approach m and the relative abundance $\widetilde{N}_{ij}^{s}$ estimated by the "reference" STOC approach. In parentheses, we present the interquartile range of this coefficient. These quantities are calculated for the set of species only monitored in the ACT survey and for the set of species not monitored in this survey.

Ratio	Species only in ACT	Species not monitored in ACT
$\widetilde{N}_{ij}^{a+\ell}$	0.55 (0.38 – 0.68)	0.35 (0.19 – 0.47)
$\widetilde{N}_{ij}^{a'+\ell}$	0.54 (0.25 – 0.61)	0.28 (0.08 – 0.40)
$\widetilde{N}_{ij}^{a}$	0.27 (0.13 – 0.49)	—
$\widetilde{N}_{ij}^{a'}$	0.06 (-0.07 – 0.23)	—
$\widetilde{N}_{ij}^{\ell 1}$	0.29 (0.24 – 0.55)	0.11 (0.06 – 0.22)
$\widetilde{N}_{ij}^{\ell 2}$	0.44 (0.35 – 0.51)	0.38 (0.13 – 0.46)

ween the estimates $\widetilde{N}_{ij}^{\ell+a}$ obtained with the full standardized dataset and the estimates $\widetilde{N}_{ij}^{\ell+a'}$ obtained with the reduced standardized dataset (median Pearson's $R = 0.84$, IQR = 0.81 – 0.90). This illustrates clearly the gain of precision obtained by combining the small standardized dataset with a large amount of opportunistic data, which we demonstrated in section 3.1. The very fine-grained distribution of observations contained in the opportunistic dataset can more efficiently predict site-specific variation in relative abundance than can the standardized dataset.

We investigated the ability of our method to estimate the relative abundance of species not monitored in the ACT survey. Note that the between-site variance of the log relative abundance estimated with our method $\widetilde{N}_{ij}^{a+\ell}$ was larger in average for the species monitored in the ACT survey (median = 2.41, IQR = 1.1 – 104) than for the species not monitored in this survey (median = 1.15, IQR = 1.04 – 1.34), which resulted in smaller Pearson's coefficient for the latter species (Tab. 2). Our approach performed better than the approaches based on the dataset a or $\ell 1$ alone. The predictive power of our approach and the approach $\ell 2$ were similar. Actually, the log observational intensity estimated in a site by our approach for the LPO dataset was strongly correlated with the logarithm of the total number of birds detected in this site (Pearson's $R = 0.85$), which supports to some extent the common practice of biologists to use the total number of birds detected in a place as a measure of the observational intensity.

5 Discussion

5.1 Overview

We propose a general approach to estimate relative abundances of multiple species on multiple "sites" (corresponding to different times and/or locations) by combining one or several datasets collected according to some standardized protocol with one or several datasets of opportunistic nature. The estimation is performed with the generalized linear model (11). This modeling relies on several assumptions, including : (i) the datasets have the same spatiotemporal extent, (ii) the individuals of the monitored species do not cluster into large groups, (iii) either the habitat types are known or the observational bias towards some habitat types are the same across the different sites. In particular, the third hypothesis is quite restrictive and handling cases where it is not met requires significant additional modeling.

We have demonstrated both theoretically (under the assumption that the model is well-specified) and numerically on some datasets, that combining opportunistic data with standardized surveys produces more reliable estimates of the relative abundances than either dataset alone. In particular, we observe an improvement in our example Section 4 even if the above hypothesis (iii) is probably violated. We have also shown that combining opportunistic data with standardized data allows for estimating relative abundance for species which are not monitored in the standardized dataset.

Our approach for combining opportunistic data with survey data is quite general : It requires to be

extended in order to overcome the current limitations (see the discussion in the next section) and to be adapted to the specifics of each case study. Yet, we highlight two already promising applications of our framework. First, we emphasize that our framework can be readily used to estimate temporal changes. In such cases, the "sites" j correspond to different times j and E_{j1} represent the parameters describing the unknown observational intensity at time j for the opportunistic dataset. For temporal variation, biased attention for some habitats in the opportunistic dataset will meet the hypothesis (iii) as long as this biased attention is constant over time. As explained in Section 2.2, such biases will be entirely captured in the estimation of the P_{ik}. For example, the accuracy of bird population trends for France will be considerably improved by the addition of opportunistic data to the current Breeding Bird Surveys.

Another very interesting feature of our framework is its ability to estimate the relative abundance of very rare species, even if these species are not monitored with a scheme with known sampling effort. This has important practical implications. For example, Guisan et al. (2006) noted "in a sample of 550 plots surveyed in a random-stratified way based on the elevation, slope, and aspect of the plot during two consecutive summers in the Swiss Alps (704.2 km^2), not one occurrence of the rare and endangered plant species *Eryngium alpinum* L. was recorded. This was despite the species being easily detectable if present and independent records of the species existing in the area within similar vegetation types." Our framework would be very useful in this context. In particular, if a citizen science program collects opportunistic data on this species along with some other more common species, then the relative abundance of the rare species can be estimated by combining these opportunistic data with standardized surveys monitoring the same common species.

5.2 Limitations and extensions

We derived from our analysis Section 2.1 a model based on the Poisson distribution. In practice, we may observe some overdispersion in the data. Causes of overdispersion include clustering of individuals, spatial auto-correlation, identification errors, etc. It is then wise to account for overdispersion in the modeling (see Section 4).

The main assumption in our modeling (1) is that the observational bias O_{ijk} can be decomposed into $O_{ijk} = P_{ik}E_{jk}$. As explained in Section 2.2, this mainly amounts to assume that the habitat types are known or the observational bias towards some habitat types are the same across the different sites. This assumption will not be met in many cases and we can expect a significant improvement by taking habitat types heterogeneity into account. This issue requires a significant additional modeling and it will be developed elsewhere.

In our estimation framework, we did not take into account any variable affecting the distribution of the relative abundance in the different sites. However, it is well-known that there might be a spatial (if the "sites" are spatial units) or temporal (if the "sites" are time units) autocorrelation in the densities. For example, it is frequent that if the abundance of a given species is high in a given spatial unit, it will also be high in neighboring units. Moreover, spatial units with a similar environmental composition will often be characterized by similar abundances. Explicitly accounting for these patterns in the estimation process could lead to an increased accuracy of the estimation (by reducing the effective number of parameters). This could be done by modeling the relative abundances $\widetilde{N}_{ij}$ as a function of environmental variables, or as a function of spatial effects (e.g. using conditional autoregression effects in a hierarchical model, see Banerjee et al., 2004). Alternatively, it is possible to maximize a regularized log-likelihood, i.e. to maximize for example :

$$\log \mathcal{L} - \sum_{i=1}^{I} \sum_{j=1}^{J} \sum_{m=1}^{J} \nu \pi_{jm} (\widetilde{N}_{ij} - \widetilde{N}_{im})^2$$

where $\mathcal{L}$ is the likelihood of the model, π_{jm} is a measure of "environmental and spatial proximities" between the unit j and the unit m, and ν is a positive parameter that determines the strength of the penalty. The proximities could be of any sort (e.g. taking the value 1 if the two spatial units are neighbours, and 0 otherwise ; inverse Euclidean distances between the units in the space defined by the environmental variables, etc.). This kind of regularization would reduce the number of effective parameters in the model and thereby increase the accuracy of the estimation (for example, see Malbasa and Vucetic, 2011).

Our statistical approach relies on the assumption that the measurement errors (identification errors, false positive) were negligible. This is a common assumption in this type of study, although recent studies

seem to indicate that (i) even a small number of false positives can lead to biases in estimates (Royle and Link, 2006), and (ii) even highly trained professionals may be subject to such errors (e.g. McClintock et al., 2010). As a solution to this problem, Miller et al. (2011) proposed to combine data collected using different approaches characterized by different probabilities of identification errors (e.g. hear counts vs. visual counts). This approach has not yet been thoroughly tested though, especially in the context of (relative) abundance estimation. Taking into account measurement errors in our framework, e.g. by integrating the approach of Miller et al. (2011), still requires further study.

The detectability of a given species is not necessarily constant across sites j in the standardized dataset, as documented in the literature (Link and Sauer, 1997; MacKenzie and Kendall, 2002). This unaccounted variation of detection probability will result into an unaccounted variation of the observational intensity. Because the knowledge of this intensity plays a crucial role in the fit of the model, such errors may bias the estimates if this variation of detection probability is structured according to some exogenous variables (e.g. habitat types). Many statistical frameworks based on a particular sampling design have been suggested to estimate detectability, such as using mixture models based on repeated counts (Royle, 2004). Further work is required to adapt such methods to our proposed framework.

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Références

Aarts, G., Fieberg, J., and Matthiopoulos, J. Comparative interpretation of count, presence–absence and point methods for species distribution models. *Methods in Ecology and Evolution* **3,** 177–187.

Banerjee, S., Carlin, B., and Gelfand, A. (2004). *Hierarchical modeling and analysis for spatial data.* Boca Raton, Florida : Chapman and Hall/CRC.

Bishop, J., Venables, W. N., and Wang, Y.-G. (2004). Analysing commercial catch and effort data from a penaeid trawl fishery : a comparison of linear models, mixed models, and generalised estimating equations approaches. *Fisheries Research* **70,** 179–193.

Boutin, J.M., Roux, D., and Eraud, C. (2003). Breeding bird monitoring in France : the ACT survey. *Ornis Hungarica* **12,** 1–2.

Boyce, M. and McDonald, L. (1999). Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution* **14,** 268–272.

Buckland, S., Anderson, D., Burnham, K., and Laake, J. (1993). *Distance Sampling : Estimating Abundance of Biological Populations.* Boca Raton, Florida : Chapman and Hall.

Cressie, N. (1993). Statistics for Spatial Data Wiley.

Dickinson, J. L., Shirk, J., Bonter, D., Bonney, R., Crain, R. L., Martin, J., Phillips, T., and Purcell, K. (2012). The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment* **10,** 291–297.

Dickinson, J. L., Zuckerberg, B., and Bonter, D. N. (2010). Citizen science as an ecological research tool : challenges and benefits. *Annual Review of Ecology, Evolution, and Systematics* **41,** 149–172.

Fithian, W. and Hastie, T. (2013). Finite-sample equivalence in statistical models for presence-only data. *The Annals of Applied Statistics* **7,** 1917–1939.

Fithian, W., Elith, J., Hastie, T., and Keith, D. (2014). Bias correction in species distribution models : pooling survey and collection data for multiple species. *Methods in Ecology and Evolution* to appear.

Gibbons, D. W., Donald, P. F., Bauer, H.-G., Fornasari, L., and Dawson, I. K. (2007). Mapping avian distributions : the evolution of bird atlases. *Bird Study* **54,** 324–334.

Guisan, A., Broennimann, O., Engler, R., Vust, M., Yoccoz, N. G., Lehmann, A., and Zimmermann, N. E. (2006). Using niche-based models to improve the sampling of rare species. *Conservation Biology* **20,** 501–511.

Hochachka, W. M., Fink, D., Hutchinson, R. A., Sheldon, D., Wong, W.-K., and Kelling, S. (2012). Data-intensive science applied to broad-scale citizen science. *Trends in Ecology & Evolution* **27,** 130–137.

Jiguet, F., Devictor, V., Julliard, R., and Couvet, D. (2012). French citizens monitoring ordinary birds provide tools for conservation and ecological sciences. *Acta Oecologica* **44,** 58–66.

Julliard, R., Jiguet, F., and Couvet, D. (2004). Common birds facing global changes : what makes a species at risk ? *Global Change Biology* **10,** 148–154.

Kéry, M., Dorazio, R., Soldaat, L., van Strien, A., Zuiderwijk, A., and Royle, J. (2009). Trend estimation in populations with imperfect detection. *Journal of Applied Ecology* **46,** 1163–1172.

Le Cam, L. (1960) An Approximation Theorem for the Poisson Binomial Distribution. *Pacific Journal of Mathematics* **10** (4), 1181–1197

Link, W. and Sauer, J. (1997). Estimation of population trajectories from count data. *Biometrics* **53,** 488–497.

MacKenzie, D. I. and Kendall, W. L. (2002). How should detection probability be incorporated into estimates of relative abundance ? *Ecology* **83,** 2387–2393.

MacKenzie, D. I., Nichols, J. D., Sutton, N., Kawanishi, K., and Bailey, L. L. (2005). Improving inferences in population studies of rare species that are detected imperfectly. *Ecology* **86,** 1101–1113.

Malbasa, V. and Vucetic, S. (2011). Spatially regularized logistic regression for disease mapping on large moving populations. In *Proceedings of the 17th ACM SIGKDD international conference on Knowledge discovery and data mining*, pages 1352–1360. ACM.

Maunder, M. and Punt, A. (2004). Standardizing catch and effort data : a review of recent approaches. *Fisheries Research* **70,** 141–159.

Miller, D.A., and Nichols, J.D., and McClintock, B.T., Grant, E.H.C., Bailey, L.L., and Weir, L.A. (2011). Improving occupancy estimation when two types of observational error occur : non-detection and species misidentification. *Ecology* **92,** 1422–1428.

McClintock, B.T., Bailey, L.L., Pollock, K.H., and Simons, T.R. (2010). Experimental investigation of observation error in anuran call surveys. *The Journal of Wildlife Management* **74,** 1882–1893.

Phillips, S., Dudík, M., Elith, J., Graham, C., Lehmann, A., Leathwick, J., and Ferrier, S. (2009). Sample selection bias and presence-only distribution models : implications for background and pseudo-absence data. *Ecological Applications* **19,** 181–197.

R Core Team (2013). *R : A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Renner, I.W. and Warton, D.I. (2013). Equivalence of MAXENT and Poisson Point Process Models for Species Distribution Modeling in Ecology. *Biometrics* **69,** 275–281.

Royle, J. and Link, W.A. (2006). Generalized site occupancy models allowing for false positive and false negative errors. *Ecology* **87,** 835–841.

Royle, J. (2004). N-mixture models for estimating population size from spatially replicated counts. *Biometrics* **60,** 108–115.

Seber, G. (1982). *The estimation of animal abundance and related parameters.* Charles Griffin & company ltd.

van Strien, A. and Pannekoek, J. (2001). Indexing european bird population trends using results of national monitoring schemes : a trial of a new method. *Bird Study* **48,** 200–213.

van Swaay, C. A., Nowicki, P., Settele, J., and van Strien, A. J. (2008). Butterfly monitoring in europe : methods, applications and perspectives. *Biodiversity and Conservation* **17,** 3455–3469.

Williams, B., Nichols, J., and Conroy, M. (2002). *Analysis and management of animal populations : modeling, estimation, and decision making.* San Diego, California : Academic Press.

Yesson, C., Brewer, P. W., Sutton, T., Caithness, N., Pahwa, J. S., Burgess, M., Gray, W. A., White, R. J., Jones, A. C., Bisby, F. A., et al. (2007). How global is the global biodiversity information facility ? *PLoS One* **2,** e1124.

Yoccoz, N., Nichols, J., and Boulinier, T. (2001). Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution* **16,** 446–453.

A Link with thinned-Poisson processes

In Section 2.1, we described a first modeling of the count data X_{ijk} leading to our model (1). In this appendix, we explain how the model (1) can also be motivated by another point of view relying on the inhomogeneous point process (IPP, see Cressie, 1993). Indeed, IPPs have recently been shown to be a central approach to model species distribution in ecology. Aarts et al. (2012) have shown the close connections existing between IPPs and resource selection functions, a commonly used approach to model habitat selection by the wildlife (Boyce and McDonald, 1999). Moreover, IPPs have also been shown to generalize other statistical approaches commonly used to model species distribution, such as the MaxEnt approach (Renner and Warton, 2013) or the classical logistic regression (Fithian and Hastie, 2013). We compare the IPP with our approach in this section.

The framework of IPPs suppose that the individuals of the species i are distributed on a domain $\mathcal{D}$ according to a Poisson point process with intensity $\lambda_i(s)$. If we assume that the individual at location s is detected and recorded in the dataset k with probability $b_{ik}(s)$, then the individuals of the species i recorded in the dataset k are distributed according to a Poisson point process with intensity $\lambda_i(s)b_{ik}(s)$. The multiplication of $\lambda_i(s)$ with $b_{ik}(s)$ results in a "thinning" of the IPP ; for this reason, the resulting point process is sometimes called thinned-Poisson process (e.g. Fithian et al., 2014). Note that in the context of IPPs, each individual is supposed to be counted at most once in each dataset (undercounting). On the contrary, in Section 2.1, we allowed multiple counts of a single individual during the multiple visits in a site, which makes our development more sensible for studies characterized by a strong observational intensity (which is generally the case of citizen science data).

However, even with this difference, our model (1) can be motivated in the context of IPPs. We can adopt different points of view for estimating relative abundances with this modeling based on IPPs. A first point of view is to introduce a model for the abundance intensities $\lambda_i(s)$ and the probabilities $b_{ik}(s)$ and then estimate these quantities accordingly. Such a point of view has been successfully developed in a simultaneous and independent work by Fithian et al. (2014) : They model the abundances intensities by $\lambda_i(s) = e^{\alpha_i + \beta_i^T x(s)}$ with $x(s)$ some observed environmental variables, the probabilities by $b_{i1}(s) = e^{\gamma_i + \delta^T z(s)}$ with $z(s)$ some other observed environmental variable and $b_{i0}(s) = 1$ at locations where survey data are available and $b_{i0}(s) = 0$, else. The abundance intensities are then estimated by $\widehat{\lambda}_i(s) = e^{\widehat{\alpha}_i + \widehat{\beta}_i^T x(s)}$, with $\widehat{\alpha}_i$ and $\widehat{\beta}_i$ some penalized maximum likelihood estimators of α_i and β_i.

An alternative point of view, which corresponds to the point of view developed in this paper, is not to try to infer the intensities $\lambda_i(s)$ for each s, but instead, to work at the scale of a whole site $S_j \subset \mathcal{D}$ and infer the mean abundance $\Lambda_{ij} = \int_{S_j} \lambda_i(s)\, ds$ of the species i on S_j. An important feature is that we do not model the abundance intensities $\lambda_i(s)$ and the probabilities $b_{ik}(s)$ in terms of some observed

environmental variables, but rather simply assume some structural properties on these functions. In particular, the mean abundance Λ_{ij} in the site j is not assumed to be completely driven by some observed environmental variables.

Let us explain how the model (1) can arise in such a context. Let us denote by $d_{ij}(s) = \lambda_i(s)/\Lambda_{ij}$ the probability density distribution describing the probability for a given individual of the species i in the site j to be located in $s \in S_j$. The number X_{ijk} of individuals of the species i counted in the site j in the dataset k is then distributed according to

$$X_{ijk} \sim \text{Poisson}\left(\Lambda_{ij} O_{ijk}\right) \quad \text{with} \quad O_{ijk} = \int_{S_j} d_{ij}(s) b_{ik}(s)\, ds\,.$$

Let us describe some scenarii, where the observational bias O_{ijk} can be decomposed as $O_{ijk} = P_{ik}E_{jk}$, leading to the model (1).

In the three examples below, we will assume that the detection/reporting probability $b_{ik}(s)$ can be decomposed in

$$b_{ik}(s) = p_{ik}\phi_k(s) \tag{18}$$

with $\phi_k(s)$ not depending on i. This means that the detection/reporting bias $b_{ik}(s)/b_{1k}(s) = p_{ik}/p_{1k}$ towards the species i in the dataset k is independent of the location s (in other words the functions $b_{1k}(s), \dots, b_{Ik}(s)$ are proportional one to the others). When this property is met we have the decomposition

$$O_{ijk} = p_{ik} \int_{S_j} d_{ij}(s)\phi_k(s)\, ds.$$

The decomposition does not give a decomposition $O_{ijk} = P_{ik}E_{jk}$ in general. Yet, such a decomposition arises in the three scenarii described below (which are the counterparts of the three examples described in Section 2.2).

Example 1 : sites with homogeneous habitat type. Assume that the species intensity ratios $\lambda_i(s)/\lambda_{i'}(s)$ depend on the species i, i' and the site j, but not on the location $s \in S_j$. Such a property is likely to be met if the site j has an homogeneous habitat type. In this case, we have $\lambda_i(s)/\lambda_{i'}(s) = \Lambda_{ij}/\Lambda_{i'j}$ and hence $\lambda_i(s) = \Lambda_{ij}g(s)$ for all i and $s \in S_j$. Then, we have

$$O_{ijk} = P_{ik}E_{jk} \quad \text{with} \quad P_{ik} = p_{ik} \quad \text{and} \quad E_{jk} = \int_{S_j} g(s)\phi_k(s)\, ds.$$

Example 2 : observations with known habitat type. In this example, we assume that for each observation we know in which habitat type $h(s)$ it has occurred (in particular, it will be the case if we know the location s of each observation). Exactly as in the Example 2 in Section 2.2, we define $\widetilde{k}$ as the couple $\widetilde{k} = (h, k)$. Assume that the density distribution $d_{ij}(s)$ depends on the species i only through the habitat $h(s)$ of s : For any i, i' and $s, s' \in S_j$ such that $h(s) = h(s')$ we have $d_{ij}(s)/d_{i'j}(s) = d_{ij}(s')/d_{i'j}(s')$. In this case, we have a decomposition $d_{ij}(s) = \alpha_{ih(s)}g(s)$ for all $s \in S_j$. Let us denote by $S_{jh} = \{s \in S_j :\ h(s) = h\}$ the portion of the site S_j with habitat type h. For any i, j and $\widetilde{k} = (h, k)$, the counts $X_{ij(h,k)}$ of individuals of the species i in the habitat h in the site j for the dataset k is distributed according to

$$X_{ij(h,k)} \sim \text{Poisson}\left(\Lambda_{ij} P_{i(h,k)} E_{j(h,k)}\right) \quad \text{with} \quad P_{i(h,k)} = \alpha_{ih} p_{i(h,k)} \quad \text{and} \quad E_{j(h,k)} = \int_{S_{jh}} g(s)\phi_{(h,k)}(s)\, ds.$$

We then have the decomposition $O_{ij\widetilde{k}} = P_{i\widetilde{k}}E_{j\widetilde{k}}$ with $\widetilde{k} = (h, k)$. We emphasize that in this case the probability $p_{i(h,k)}$ appearing in the decomposition (18) is allowed to depend on the habitat type h (the bias towards some species may differ depending on the habitat type).

Example 3 : homogeneous distribution of habitat types. We do not assume anymore that the habitat type $h(s)$ for each observation is known. We assume again that we have the decomposition $d_{ij}(s) = \alpha_{ih(s)}g(s)$ for all $s \in S_j$, hence

$$O_{ijk} = p_{ik} \sum_h \alpha_{ih} \int_{S_{jh}} g(s)\phi_k(s)\, ds.$$

If we assume in addition that

$$\int_{S_{jh}} g(s)\phi_k(s)\,ds = Q_{hk}\int_{S_j} g(s)\phi_k(s)\,ds, \tag{19}$$

then

$$O_{ijk} = P_{ik}E_{jk} \quad \text{with} \quad P_{ik} = p_{ik}\sum_h \alpha_{ih}Q_{hk} \quad \text{and} \quad E_{jk} = \int_{S_j} g(s)\phi_k(s)\,ds.$$

Let us investigate when the decomposition (19) can be met. Assume first that $\phi_k(s) = \beta_{kh(s)}\gamma_k(s)$ where $\gamma_k(s)$ reflects local fluctuations independent of the habitat type. The function $g(s)\gamma_k(s)$ then represents small scale fluctuations and we can expect to have

$$\int_S g(s)\gamma_k(s)\,ds \approx q_k|S|,$$

for S large enough. It would be the case for example if $g(s)\gamma_k(s)$ was the outcome of a stationary process. We then have

$$\frac{\int_{S_{jh}} g(s)\phi_k(s)\,ds}{\int_{S_j} g(s)\phi_k(s)\,ds} \approx \frac{\beta_{hk}q_k|S_{jh}|}{\sum_h \beta_{hk}q_k|S_{jh}|}\,.$$

When the ratios $|S_{jh}|/|S_j|$ do not depend on j, the above ratio depends on h and k only, so (19) holds. This case corresponds to sites S_j all having a similar distribution of habitat types. This property will be met if the sites S_j correspond to the same location at different times j.

B Mathematical proofs

B.1 Identifiability conditions

With the notations $n_{ij} = \log(N_{ij})$, $e_{jk} = \log(E_{jk})$ and $p_{ik} = \log(P_{ik})$, the model (1) described in our paper can be recast as a classical generalized linear model

$$X_{ijk} \sim \text{Poisson}(\lambda_{ijk}), \quad \text{with } \log(\lambda_{ijk}) = n_{ij} + e_{jk} + p_{ik}.$$

The kernel of the design matrix associated with this linear regression has a dimension equal to $I + J + 1$. Therefore, we need $I + J + 1$ constraints to ensure the identifiability of the model.

B.2 Properties of the estimators

The negative log-likelihood of the parameters $(\widetilde{N}_{ij}, \widetilde{E}_{jk}, \widetilde{P}_{ik})$ is

$$\mathcal{L} = \sum_{i\in I}\sum_{j\in J}\sum_{k\in\{0,1\}} \left(\widetilde{N}_{ij}\widetilde{E}_{jk}\widetilde{P}_{ik} - X_{ijk}\log(\widetilde{N}_{ij}\widetilde{E}_{jk}\widetilde{P}_{ik}) + \log(X_{ijk}!)\right)$$

where the parameters $\{\widetilde{E}_{j0},\ j \in J\}$ and $\{\widetilde{P}_{i0},\ i \in I\}$ are known, $\widetilde{P}_{10} = 1$ and $\widetilde{P}_{i1} = 1$ for all $i \in I$.

To keep the mathematical analysis of the maximum likelihood estimators comprehensible, we focus below on the case where the $\widetilde{P}_{i0}$ are known. The maximum likelihood estimators of $\widetilde{N}_{ij}$ and $\widetilde{E}_{j1}$ are then the solutions of

$$\widehat{N}_{ij} = \frac{X_{ij0} + X_{ij1}}{\widetilde{P}_{i0}\widetilde{E}_{j0} + \widehat{E}_{j1}} \quad \text{and} \quad \widehat{E}_{j1} = \frac{X_{\#j1}}{\widehat{N}_{\#j}}\,, \tag{20}$$

where $X_{\#jk} = \sum_i X_{ijk}$ and $\widehat{N}_{\#j} = \sum_i \widehat{N}_{ij}$.

We first treat the simplest case where the $\widetilde{P}_{i0}$ are all equal.

B.2.1 Case of constant ratios P_{i0}/P_{i1}

We consider in this paragraph the case where $\widetilde{P}_{i0} = \widetilde{P}_{10}$ for all $i \in I$. This corresponds to the case where for all the species i, the detection/reporting probability ratios P_{i0}/P_{i1} are the same and equal to P_{10}/P_{11}. We derive from (20)

$$\widehat{N}_{\#j} = \frac{X_{\#j0} + X_{\#j1}}{\widetilde{E}_{j0} + \widehat{E}_{j1}}$$

and inserting this expression in the formula for $\widehat{E}_{j1}$ we obtain $\widehat{E}_{j1} = \widetilde{E}_{j0} X_{\#j1}/X_{\#j0}$. As a consequence, we obtain the closed-form expression for $\widehat{N}_{ij}$

$$\widehat{N}_{ij} = \frac{X_{ij0} + X_{ij1}}{X_{\#j0} + X_{\#j1}} \times \frac{X_{\#j0}}{\widetilde{E}_{j0}}. \tag{21}$$

According to the strong law of large numbers for Poisson processes, we have

$$\widehat{N}_{ij} \overset{E_{j1}\to\infty}{\to} \frac{\widetilde{N}_{ij}}{\widetilde{N}_{\#j}} \times \frac{X_{\#j0}}{\widetilde{E}_{j0}} \tag{22}$$

and

$$\mathrm{var}(\widehat{N}_{ij}) \overset{E_{j1}\to\infty}{\to} \left(\frac{\widetilde{N}_{ij}}{\widetilde{N}_{\#j}}\right)^2 \times \frac{\widetilde{N}_{\#j}}{\widetilde{E}_{j0}} = \frac{\widetilde{N}_{ij}}{\widetilde{E}_{j0}} \times \frac{N_{ij}P_{i0}}{\sum_l N_{lj}P_{l0}}.$$

If we estimate $\widetilde{N}_{ij}$ with the sole "known-effort" data X_{ij0}, the maximum likelihood estimator is given by $\widehat{N}^0_{ij} = X_{ij0}/\widetilde{E}_{j0}$ and its variance equals $\mathrm{var}(\widehat{N}^0_{ij}) = \widetilde{N}_{ij}/\widetilde{E}_{j0}$. We can then compare the variance of $\widehat{N}_{ij}$ and $\widehat{N}^0_{ij}$

$$\mathrm{var}(\widehat{N}_{ij}) \overset{E_{j1}\to\infty}{\sim} \mathrm{var}(\widehat{N}^0_{ij}) \times \frac{N_{ij}P_{i0}}{\sum_l N_{lj}P_{l0}}. \tag{23}$$

B.2.2 Case of arbitrary ratios P_{i0}/P_{i1}

We no longer assume that the $\widetilde{P}_{i0}$ are all equal. In this case, we have no closed-form formula for $\widehat{N}_{ij}$ but we can compute a first-order expansion of $\widehat{N}_{ij}$ in terms of the inverse of $X_{\#j1}$.

The first step is to check that $\widehat{N}_{\#j}$ is upper-bounded independently of the X_{ij1}. When $P_{i0} > 0$ for all i (which means that the same species are monitored in the datasets 0 and 1), we have from (20)

$$\widehat{N}_{ij} \leq \frac{X_{ij0} + X_{ij1}}{\min_i(\widetilde{P}_{i0}\widetilde{E}_{i0}) + X_{\#j1}/\widehat{N}_{\#j}}.$$

Summing these inequalities we obtain the upper-bound

$$\widehat{N}_{\#j} \leq X_{\#j0}/\min_i(\widetilde{P}_{i0}\widetilde{E}_{j0})$$

which does not depend on X_{ij1}. The case where $P_{i0} = 0$ for some i can be treated similarly : splitting apart the indices in $I_0 = \{i \in I : P_{i0} = 0\}$ and those out of I_0, we get from (20)

$$\widehat{N}_{\#j} \leq \frac{\sum_{i\in I_0}(X_{ij0} + X_{ij1})}{X_{\#j1}/\widehat{N}_{\#j}} + \frac{\sum_{i\notin I_0}(X_{ij0} + X_{ij1})}{\min_{i\notin I_0}(\widetilde{P}_{i0}\widetilde{E}_{i0}) + X_{\#j1}/\widehat{N}_{\#j}}.$$

This inequality is equivalent to

$$\widehat{N}_{\#j}\left(1 - \frac{\sum_{i\in I_0}(X_{ij0} + X_{ij1})}{X_{\#j1}}\right) \leq X_{\#j0}/\min_{i\notin I_0}(\widetilde{P}_{i0}\widetilde{E}_{j0}).$$

In the asymptotic $E_{j1} \to \infty$ we obtain the asymptotic upper-bound

$$\widehat{N}_{\#j} \leq \frac{X_{\#j0}}{\min_{i\notin I_0}(\widetilde{P}_{i0}\widetilde{E}_{j0})} \times \frac{\sum_{i\in I}\widetilde{N}_{ij}}{\sum_{i\in I\setminus I_0}\widetilde{N}_{ij}}.$$

Now that we have checked that $\widehat{N}_{\#j}$ is (asymptotically) upper-bounded independently of the X_{ij1}, we can write a first-order expansion of the formula (20)

$$\widehat{N}_{ij} = \frac{(X_{ij0}+X_{ij1})\widehat{N}_{\#j}}{X_{\#j1}} - \frac{(X_{ij0}+X_{ij1})\widehat{N}_{\#j}^2 \widetilde{P}_{i0}\widetilde{E}_{j0}}{X_{\#j1}^2} + O\left(\frac{X_{ij1}}{X_{\#j1}^3}\right). \tag{24}$$

Summing these expansions over $i \in I$ and simplifying the expression gives

$$\widehat{N}_{\#j} = \frac{X_{\#j0}X_{\#j1}}{\widetilde{E}_{j0}\sum_l \widetilde{P}_{l0}(X_{lj0}+X_{lj1})}\left(1+O\left(\frac{1}{X_{\#j1}}\right)\right).$$

Plugging this formula in (24) gives

$$\begin{aligned}\widehat{N}_{ij} \quad &= \quad \frac{X_{ij0}+X_{ij1}}{\sum_l \widetilde{P}_{l0}(X_{lj0}+X_{lj1})} \times \frac{X_{\#j0}}{\widetilde{E}_{j0}} \times \left(1+O\left(\frac{1}{X_{\#j1}}\right)\right) \\ &\overset{E_{j1}\to\infty}{\to} \quad \frac{\widetilde{N}_{ij}}{\sum_l \widetilde{P}_{l0}\widetilde{N}_{lj}} \times \frac{X_{\#j0}}{\widetilde{E}_{j0}},\end{aligned}$$

where the last limit follows again from the law of large numbers for Poisson processes. Computing the asymptotic variance when $E_{j1} \to \infty$, we find after simplification

$$\mathrm{var}(\widehat{N}_{ij}) \overset{E_{j1}\to\infty}{\to} \frac{\widetilde{N}_{ij}^2}{\sum_l \widetilde{P}_{l0}\widetilde{N}_{lj}\widetilde{E}_{j0}} = \frac{\widetilde{N}_{ij}}{\widetilde{P}_{i0}\widetilde{E}_{j0}} \times \frac{P_{i0}N_{ij}}{\sum_l P_{l0}N_{lj}}. \tag{25}$$

As in the previous case, we can compare this variance to the variance of the maximum likelihood estimator $\widehat{N}_{ij}^0 = X_{ij0}/(\widetilde{P}_{i0}\widetilde{E}_{j0})$ obtained by estimating $\widetilde{N}_{ij}$ with the sole values X_{ij0}. The variance of $\widehat{N}_{ij}^0$ being $\mathrm{var}(\widehat{N}_{ij}^0) = \widetilde{N}_{ij}/(\widetilde{P}_{i0}\widetilde{E}_{j0})$, we obtain the reduction of variance

$$\mathrm{var}(\widehat{N}_{ij}) \overset{E_{j1}\to\infty}{\sim} \mathrm{var}(\widehat{N}_{ij}^0) \times \frac{P_{i0}N_{ij}}{\sum_l P_{l0}N_{lj}}. \tag{26}$$